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In Situ Spawning of Hydrothermal Vent Tubeworms (*Riftia pachyptila*)

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Riftia pachyptila, *the giant vestimentiferan tubeworm, dominates the biomass of many hydrothermal vent sites in the Gulf of California (Guaymas Basin) and on the East Pacific Rise and Galapagos Spreading Center (1). The worms typically occur in large clumps or thickets as mixed populations of males and females. On a dive series made by the submersible* Alvin *in the vicinity of 9°50′ N on the East Pacific Rise, I observed spawning tubeworms while I was sampling associated fauna. This note presents a brief account of the spawning activity.*

A population of adult vestimentiferans (length greater than 1 m) colonizes a 10 m high basalt pillar at 9°49.59′ N, 104°17.37′ W (2511 m depth) within the Venture Hydrothermal Fields (2). Tubeworms cover most of the surface of the pillar and are relatively uniform in size and so densely packed that they present a cylindrical face of red plumes around the pillar. The site, known as Dudley's Pillar, is marked by a round white lid labeled "2" placed during the Haymon and Fornari expedition in May 1991.

On *Alvin* dive #2474 (6 December 1991), several *R. pachyptila* were observed to spawn during an hour of intermittent observations. Each release of gametes consisted of a small, 10–15 cm cloud of eggs or sperm; the gametes were propelled upward by a rapid, partial withdrawal of the worm into its tube. It was not possible to determine if the same individuals were spawning repeatedly. Fewer than 10 individuals comprising a small portion of the tubeworm population (covering about ⅓ to ½ m^2) were observed engaged in spawning activity. The frequency of spawning contractions of individual worms was not determined; the interval between observed spawns was about 2–3 min. Both males and females were observed spawning. After release, the cloud of eggs separated and the eggs, which were slightly negatively buoyant, were observed to sink in amongst the tubeworms. Sperm formed an apparently neutrally buoyant, milky cloud that dispersed in the current within 10 s. Mixing of egg and sperm clouds was not observed. No spawning activity was noted on a visit to the same site 3 days earlier nor on a subsequent dive to the site 4 days later (L. Mullineaux and L. Garland, pers. comm.).

Although the above observations are limited, we can infer several features of the reproductive ecology of hydrothermal vent tubeworms:

1. Spawning in *R. pachyptila* populations is not necessarily *en masse*. Only a few individuals out of a colony of hundreds were involved in the release of gametes. This observation does not preclude mass spawning by a large proportion of the population under appropriate conditions. Concurrent spawning by several individuals, both male and female, suggests synchronization of gamete release among sexually mature animals, presumably mediated by a chemical cue.

2. Spawning behavior within tubeworm populations, as described above, is intermittent, not continuous. Although this might seem patent from the lack of spawning observations during the accumulated tens of hours of observation time over the 15 years since tubeworm populations were first discovered, the possibility of continuous but inconspicuous release of gametes exists. Observations here suggest that individual spawning is best described as an acute rather than a chronic event, with the spawning period lasting on the order of hours.

3. The negative buoyancy of female gametes generates a dispersal shadow that initially lies close to the adult.

Some features of these observations must be reconciled with other studies. Cary *et al.* (3) describe spawning of female *R. pachyptila* in a shipboard pressure chamber.

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Females released streams of eggs, bound by mucus, from the gonopores over a period of 30 min. The eggs were retained in the vestimental cavity for a few minutes before the mucous binding dissolved and the eggs, positively buoyant, floated upward. In unpressurized aquaria, the same authors (3) observed male tubeworms spawning, with semen continuously flowing from the male gonopores. Though it is conceivable that release of a stream of gametes, rather than punctuated and forceful expulsion of gametes as observed *in situ*, is an alternative reproductive strategy, the observations of Cary *et al.* (3) may represent anomalous behavior as a result of trauma during collection, ascent, and depressurization. If this is the case, the positive buoyancy of the eggs may be an artifact of premature gamete release. Southward and Coates (4) suggest, based on characteristics of the acrosome, that Cary *et al.* witnessed expulsion of immature sperm.

Based on morphological criteria of modified sperm in *R. pachyptila*, Gardiner and Jones (5) suggest that this species has some form of direct sperm transfer or internal fertilization. Likewise, the presence of sperm together with eggs in the female genital tracts of *R. pachyptila* suggests the possibility of internal fertilization (6). Cary *et al.* (3) demonstrate that *R. pachyptila* sperm bundles are effective swimmers and suggest that the bundles may become anchored in the vicinity of the female gonopores or within the anterior regions of the oviducts. Southward and Coates (4) suggest that active sperm transfer is likely in a group of related vestimentiferans (*Ridgeia* spp.), and that this transfer takes place when the plumes of closely juxtaposed animals may brush against each other.

In situ observations reconciled with the literature cited above suggest the following spawning scenario in *R. pachyptila:* (1) Neutrally buoyant sperm bundles are expelled forcefully enough to be dispersed over a field of tubeworms; (2) the sperm bundles swim and attach to females, somehow mediating a spawning response in the female; (3) fertilization occurs internally immediately before spawning or externally (within the vestimental chamber?) just after release of the eggs; (4) accumulated eggs are forcefully ejected into the water column where, negatively buoyant, they spend a short period near the site of release; (5) advective conditions of the turbulent, warm-water vent environment disperse gametes and developing larvae away from the adult population.

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